

THE DOMINANT CONIFER OF THE JURASSIC PURBECK FORMATION, ENGLAND

by JANE E. FRANCIS

ABSTRACT. Fossil trees are preserved *in situ* in fossil soils in the Lower Purbeck (Upper Jurassic) strata of Dorset. Silicified tree stumps, still rooted in the soils, stand erect and protrude into the overlying limestones. Numerous trunks and branches lie on the soils, which also contain conifer shoots. The forests were dominated by one kind of conifer with wood, named here as *Protocupressinoxylon purbeckensis* sp. nov., foliage belonging to the species *Cupressinocladus valdensis* (Seward) Seward and with male cones yielding *Classopollis* pollen. A reconstruction of the anatomy and habit of the tree is given. The Lower Purbeck palaeoclimate is discussed using the evidence of tree growth rings and the character of the associated sediments.

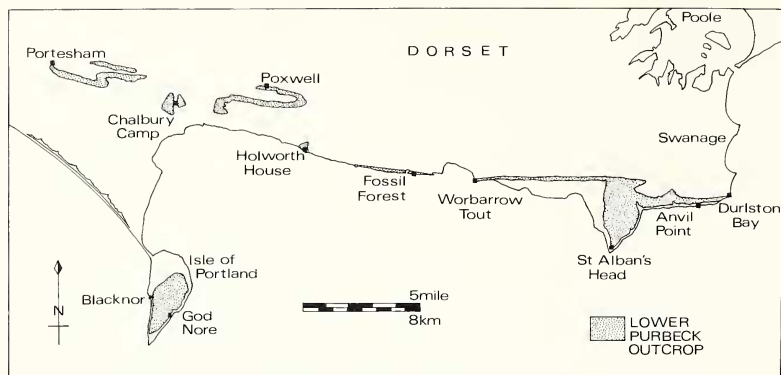
THE Lower Purbeck Formation of Dorset represents a sequence of intertidal and supratidal deposits formed during minor transgressive and regressive phases at the edge of a very shallow hypersaline gulf (West 1975). During the first regressive phase the pelletoid silts which were deposited in the lagoon became subaerially exposed and a thin soil developed, now represented by the carbonaceous marl of the Lower Dirt Bed. This soil supported a conifer forest (Strahan 1898; Arkell 1947) which was subsequently drowned by a rapid transgression, recreating extensive tidal flats with large stromatolitic growths (Brown 1963; Pugh 1968). In a second regressive phase gypsum and caliche breccia formed as the area became desiccated in the semi-arid climate (West 1975), and gradually the soil of the Great Dirt Bed formed. This soil incorporated pebbles derived from the underlying lithified limestone including black pebbles which are similar to modern blackened limestone pebbles found on the margins of hypersaline lakes (Ward *et al.* 1970). A closed forest of conifers and cycadophytes became established, bordered by a shallow gulf to the east and an ephemeral inland lake with charophytes in the west (West 1975; Barker *et al.* 1975). This forest was also rapidly submerged by hypersaline water and the tree stumps and fallen logs became covered with algal-bound sediment (Strahan 1898). Hypersaline water eventually covered the whole area and the main Purbeck evaporite deposits formed (West 1964).

This sequence of events is now represented by algal stromatolitic limestones forming algal heads and non-laminated hummocks, and thinly-bedded pelletoid limestones, some with calcite pseudomorphs after gypsum. Interbedded dark carbonaceous marls of the Lower and Great Dirt Bed represent the former forest soils (text-fig. 2). The erect conifer stumps, fallen trunks, and cycadophyte stems became silicified and remain preserved within circular 'burrs' or domes of stromatolitic limestone (Pl. 38, figs. 2, 4, 5). Silicified wood is abundant in the Lower Dirt Bed of mainland Dorset and in the Great Dirt Bed on both the mainland and the Isle of Portland. Although trees grew in the former dirt bed on Portland they were not petrified but rotted away, leaving tubular cavities within the overlying stromatolitic Hard Cap limestone (text-fig. 2).

At most of the sites examined the conifer foliage is not preserved within the dark, marly dirt beds but an exception is the Great Dirt Bed at God Nore, Portland (text-fig. 1), where the dirt bed is reworked and resedimented. At this site there are a few organic-rich laminae, each of about 10 cm² in area, scattered throughout the Great Dirt Bed and on which compressed, fragmentary conifer shoots and male cones were found. No female cones were found. The matrix also yielded a fairly rich miospore assemblage. More complete conifer shoots are preserved in the overlying limestones.

The aim of this paper is to present a reconstruction of the anatomy and habit of the most abundant conifer species which grew in the Lower Purbeck forests.

Valuable information about the 'fossil forests' was recorded by geologists in the nineteenth century,



TEXT-FIG. 1. Map showing the location of some basal Purbeck exposures mentioned in the text.

particularly from quarries on Portland in which fossil trees and soils were being uncovered during a period of extensive quarrying (Webster 1826; Buckland and De La Beche 1836; Fitton 1835 and 1836; Mantell 1854). They discovered erect tree stumps in their original growth positions, often over 1 m in height and penetrating the overlying limestones. Numerous fallen trunks and branches were observed on the fossil soil, some over 10 m in length and 1.3 m in diameter. The erect stumps were shown to have roots which spread laterally through the soil, illustrated in sketches by Fitton (1836) and Buckland and De La Beche (1836). The roots never appear to penetrate the underlying hard limestone but are sharply diverted back at the base of the soil.

Damon (1884a) and Mantell (1854), amongst others, agreed that the profusion of fossil wood found on the surface of the Great Dirt Bed clearly indicated that these trees grew in as close proximity as those of a modern forest. Damon (1884a) noted, for example, that in a quarry on Portland, 7 erect tree stumps and 2 'Cycadeae' were uncovered in an area of only 'a few square yards'.

The leafy shoots of the trees were noticeably absent from major exposures of the fossil forests (Buckland and De La Beche 1836) though a single specimen of conifer foliage was illustrated by Damon (1884b) from the 'Top Cap' limestone overlying the Great Dirt Bed on Portland. It was a small shoot with scale-like leaves, tentatively identified as *Cupressinocladus*. Fitton also found an araucarian cone on the Portland cliffs which was identified as *Araucaria sphaerocarpa* by Carruthers (1866). Silicified stems of cycadophytes (Bennettitales) were often found amongst the fossil trees and were believed by some quarrymen to be fossil crows' nests which had fallen from the branches of the fossil trees! Although less numerous than the conifers these plants occur throughout the area, even where conifers are absent. It was due to the presence of such plants, which were wrongly interpreted as cycads (Cycadales), that Fitton (1835), Buckland (1829), Damon (1884a), and others first concluded that a warmer climate than at present prevailed in early Purbeck times since modern cycads occur chiefly in tropical regions. The cycadophyte stems were studied in detail by Buckland (1829) and Carruthers (1870), although their leaves are not described.

EXPLANATION OF PLATE 38

Fig. 1. Silicified tree stump at Chalbury Camp. Its roots are preserved within the Lower Dirt Bed and the trunk is surrounded by algal stromatolitic limestone of the Hard Cap. Diameter of base of trunk 92 cm.

Figs. 2, 4, 5. 'Burs' of algal stromatolitic limestone, Soft Cap, Fossil Forest. 2, trough-shaped burr which once encased a fallen trunk. Total length 4.68 m. 4, 5, circular burs which once surrounded tree stumps. 4, inner diameter 81 cm. 5, inner diameter 78 cm.

Fig. 3. Large silicified trunk reconstructed in the grounds of the Portland Heights Motel, Portland. Approximate height 2 m.



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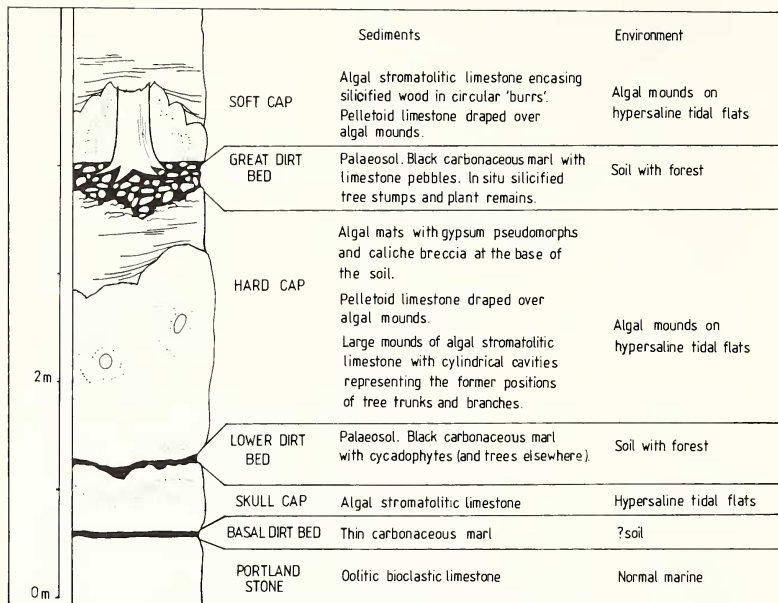


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FRANCIS, silicified trees, and 'burrs' of stromatolitic limestone



TEXT-FIG. 2. Generalized section of the basal Purbeck strata on Portland.

Many fragments of plant remains were obtained from the Portesham Charophyte Chert, the western equivalent of the Great Dirt Bed, by Barker *et al.* (1975). These include charophyte fragments, stems of *Equisetum mobergii* (Halle ex. Moller), a small portion of a scale-leaved conifer (*Brachyphyllum* sp.), fragments of silicified wood and fusain, several species of seeds assigned to the genus *Carpolithus* Schlotheim and silicified casts of part of an araucarian cone *Araucarites sizerae*.

Most of the modern work on Purbeckian plants has concerned the miospore assemblages. Couper (1958), Lantz (1958) and Norris (1969) included Purbeck limestones, shales, and clays amongst their samples for miospore analysis and used the spores and pollen for stratigraphic zonation and correlation. Their samples were dominated by *Classopollis* pollen which constituted up to 70% of the miospore assemblages and suggest a forest dominated by *Classopollis*-producing trees, though it would be dangerous to base this interpretation on miospores alone (Chaloner and Muir 1968). They found a few other pollen grains which they attributed to conifers and cycadophytes, and there were some pteridophyte spores thought to belong to the undergrowth.

METHODS

Samples of silicified wood collected for study included portions of *in situ* tree stumps, branches, and roots from both the Lower and Great Dirt Beds at localities shown in text-fig. 1 and isolated specimens from museums and quarry tips, particularly on Portland.

The silicified wood structure was studied in thin-section, requiring three mutually perpendicular sections of each tree to fully demonstrate the anatomy (transverse, radial longitudinal, and tangential longitudinal). Small

fusain fragments were obtained from the bulk maceration residue of the dirt beds. These fragments together with cleanly fractured silicified wood, were examined by SEM.

In situ conifer cuticles were picked directly from the intact shoots and male cones on limestone. Dispersed cuticle and pollen was isolated from the Great Dirt Bed matrix by bulk maceration. Small pieces of the soil matrix were subjected to acid digest with hydrochloric and then hydrofluoric acid to remove carbonates and silicates, followed by a final wash with warm hydrochloric acid to remove mineral by-products which obscured the organic matter (see Norris 1969). The cuticle was then separated from the residue by sieving with a 120 μm mesh sieve and was carefully macerated with concentrated nitric acid. Dilute ammonium hydroxide was used to remove humic matter left after oxidation. The cuticle was mounted in glycerine jelly for observation in transmitted light or dried onto stubs for SEM observation.

The fine residue containing pollen was gently macerated as before. Clay minerals of less than 5 μm in size were removed in suspension using a method based upon Stokes' Law (Jackson 1975). The spore rich residue was then dried on to SEM stubs or mounted in glycerine jelly, a few samples having been stained with Safranin O for examination with the light microscope.

SYSTEMATIC PALAEOLOGY

Order CONIFERALES

Family CHEIROLEPIDACEAE [HIRMERIACEAE]

Form-genus PROTOCUPRESSINOXYLON Eckhold 1922 (in part)

Protocupressinoxylon purbeckensis sp. nov.

Plate 39, figs. 1-11

Diagnosis. Growth rings fairly well defined, with a relatively wide zone of early wood and a narrow zone (3-4 cells) of late wood; false rings often present within what appear to be the annual increments. Files of tracheids of uniform appearance; tracheids polygonal or rounded in cross-section; average diameter of lumen 29.4 μm in early wood, 6.2 μm in late wood; wall thickness constant throughout, 9 μm .

Bordered pits on radial walls of tracheids mainly uniseriate (Pl. 39, fig. 11), biseriate opposite arrangement rare; biseriate alternate pitting absent. Pit border and aperture circular (mean diameters 17.2 μm and 6.0 μm respectively); pitting both spaced and contiguous. Contiguously arranged pits have adjacent borders touching and slightly compressed with vertical thickenings.

Rays, seen in tangential longitudinal section (Pl. 39, fig. 8), numerous, often separated by only 3 or 4 tracheids, 2-9 cells deep, mostly 3. Ray cells seen in radial longitudinal section rectangular with 2-7 small pits per crossfield; pits cupressoid with a slit-like aperture within a well developed, round border; aperture inclined at about 45° (Pl. 39, fig. 6), mean diameter 7-8 μm . Horizontal and tangential walls of ray cells thin, unpitted. Wood parenchyma absent.

Resin canals absent, but tracheids often containing a dark resinous deposit throughout the growth ring and ray cells.

Holotype: Silicified trunk, PB.11. is designated as holotype.

Location: Blacknor, Portland.

Horizon: Great Dirt Bed, Lower Purbeck Beds.

Description. Fossil wood with this structure is most common in the dirt beds and constitutes over 90% of all identifiable silicified and fusainized wood samples examined. The state of preservation is very variable in the silicified wood although structural details are particularly enhanced by remaining organic matter outlining cell walls. Fragments of fusain exhibit superbly preserved features, (Pl. 39, figs. 1-3, 5, 6). However, all measurements were taken from silicified wood as fusain exhibits an overall shrinkage of about 30%.

The contiguous pitting of the tracheid walls is the most distinguishable feature of this wood (Pl. 39, fig. 11). The pit borders always touch, sometimes retaining a circular outline, often vertically compressed but never to the extent of acquiring a polygonal outline like the pits of araucarian wood. Pit diameters vary between specimens and range from mean values of 12.5 μm to 17.6 μm , with an overall mean for all the specimens examined

of 14.3 μm . Bars of Sanio (cellulose thickenings across the tracheids) are not visible since the pits themselves are so closely packed. Biseriate rows are more common in some samples than others but the pit arrangement is always opposite. No pitting was observed on the tangential tracheid walls.

Pitting was not seen on the horizontal and tangential walls of the ray cells although they looked well enough preserved to show them. 1 to 7 cupressoid pits are visible on each crossfield though 2 or 4 are most common. The pit aperture maintains a constant orientation close to 45° throughout the whole ray and even the whole specimen (Pl. 39, fig. 3). The abundance of resin in this type of wood is particularly noticeable, being present in all cell types as either small globules (2–10 μm in diameter) or as a resinous film coating cell walls. In transverse section the resin-filled cells are scattered throughout the growth ring, not confined to the latewood zone. No resin canals occur anywhere within the wood, either original canals or those which might result from wound reaction.

Form-genus CUPRESSINOCLADUS Seward 1919
Cupressinocladus valdensis (Seward) Seward 1919

Plate 40, figs. 1–13

- 1895 *Thuites valdensis* Seward, 209, pl. 20, fig. 6.
 1919 *Cupressinocladus valdensis* (Seward) Seward, 309.
 1960 *Cupressinocladus valdensis* (Seward); Chaloner and Lorch, 236.
 1977 *Cupressinocladus valdensis* (Seward); Watson, 742, pl. 97, figs. 6–11.

Holotype: British Museum (Natural History) V.2138. from the Wealden at Ecclesbourne, Hastings.

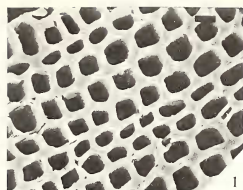
Material. Conifer shoots and dispersed cuticle were found in the Great Dirt Bed at God Nore, Portland (National Grid map reference SY690697) and in the equivalent bed at Holworth House cliff section (SY762816). More complete shoots from adjacent limestones were studied to discover leaf and branch arrangement. These specimens were obtained from museums and include PB:conf 1 from the Lower Purbeck Beds, Southwell, Portland (Portland Museum), PB:conf 2 from the Purbeck Beds, Lulworth Cove (Southampton University Geology Museum, Day collection,) PB:conf 3 from the Middle Purbeck Beds of Durlston Bay (private collection of R. Coram, Wimborne), V.4033, V.4029, V.2933, and V.2545-shoots from basal Purbeck limestones, Portland (B.M. (N.H) collections).

Description. The most complete shoot, PB:conf 1, (Pl. 40, fig. 11) is 9.6 cm long and exhibits up to 4 orders of branching with branches arising in one plane to produce a flat, frond-like shoot. Branches arise alternately at every node on the main stem and minor branchlets, but appear to be arranged in opposition on the ultimate shoots. Alternate branchlets are straight or slightly curved. The main laterals subtend an angle of about 45° to the main stem and subsequent branches subtend an angle of about 55°. The whole shoot is now strongly compressed and bears small leaves in an opposite and decussate arrangement strongly reminiscent of modern Cupressaceae, such as, for example, *Thuja plicata* D. Don.

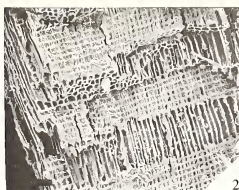
EXPLANATION OF PLATE 39

Protocupressinoxylon purbeckensis sp. nov.

- Figs. 1–3, 5, 6. Fusain from the Great Dirt Bed, God Nore, Portland. 1, transverse section. SEM $\times 130$. 2, radial longitudinal section showing tracheids crossed by medullary rays. SEM $\times 50$. 3, medullary ray cells, enlarged from fig. 2. SEM $\times 200$. 5, tangential longitudinal section. SEM $\times 50$. 6, cross-field pits on radial walls of the ray cells. SEM $\times 1000$.
 Figs. 4, 10. Silicified wood, PB.24, Great Dirt Bed, Portland. 4, radial longitudinal section showing bordered pits on radial walls of tracheids. SEM $\times 500$. 10, radial longitudinal section showing resin-filled ray cells. Light microscope $\times 50$.
 Fig. 7. Silicified wood, PB.52, Great Dirt Bed, Inmosthay Quarry, Portland. Thin section showing small knot. $\times 3.75$.
 Figs. 8, 9, 11. Silicified wood, Great Dirt Bed, Blacknor, Portland. 8, tangential longitudinal section showing ray cells 2–8 cells deep. Light microscope $\times 50$. 9, transverse section showing variable ring widths. Light microscope $\times 2.0$. 11, radial longitudinal section showing uniseriate rows of contiguous bordered pits. Light microscope $\times 145$.



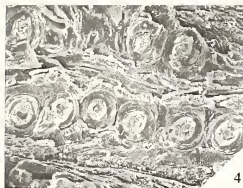
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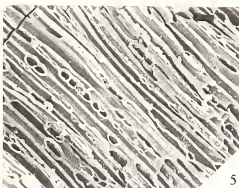
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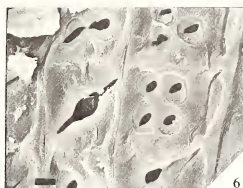
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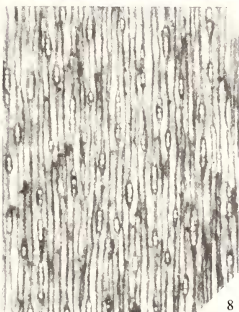
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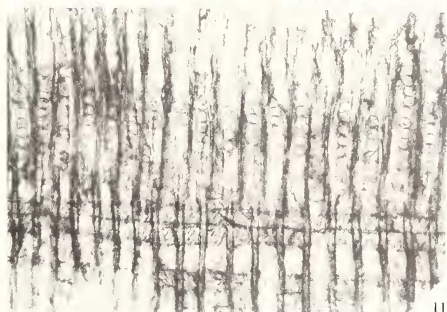
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The main axis of this specimen has elongate rectangular leaves 10 mm long, 6 mm wide and pressed close to the stem. Secondary and tertiary branchlets have shorter and narrower leaves which ultimately become square in shape, with a length and breadth of only 1 mm on the youngest shoots. The range in leaf sizes of all specimens is 1 to 10 mm in length, 1 to 6 mm in width. Each leaf on the main shoot has a short, triangular free part and a long decurrent cushion with clear grooves separating it from adjacent cushions.

The abaxial cuticle ranges from 15–20 μm thick. Both the abaxial and adaxial cuticle are covered with short, blunt papillae about 10 μm in height, though on some specimens these are less well-defined and appear merely as a slightly raised area of the cuticle. In the cuticle from the abaxial surface of the free leaf and cushion stomata are arranged in fairly well-defined files and extend over the whole leaf base, including the marginal area. Stomata are, however, absent from a small area at the leaf tip (Pl. 40, fig. 3). The stomatal rows are separated by 2 to 3 epidermal cells and there are 6–8 rows per mm laterally. The stomatal density along each file ranges from 6–9 per mm, giving a mean density of 44 per mm^2 .

Each stoma is surrounded by 4–6, but typically 5 subsidiary cells and the whole stomatal apparatus has a diameter of 70–100 μm . Each subsidiary cell bears one broad round papilla which extends into the stomatal pit so that its aperture is nearly filled by the papillae (Pl. 40, figs. 5, 8, 12). The mouth of the pit is commonly polygonal but varies from more or less round to markedly stellate. Some stomata have their openings at surface level though adjacent ones on the same cuticle have a prominent rim (Pl. 40, figs. 8, 12). The guard cells are sometimes present but are thinly cutinized and often do not survive maceration.

The epidermal cells lying between stomata of the same file are isodiametric, 20–35 μm in diameter. However, between stomatal rows the cells are usually elongate (on average 48 μm long) and arranged in longitudinal files 2 to 3 cells wide. The anticlinal walls are 8–10 μm thick. The larger elongate hypodermis cells (mean of 64 μm in length, 37 μm wide) can sometimes be seen between stomatal rows.

The free tip of the leaf is always short. One leaf on the main shoot had a tip 2.6 mm long and a decurrent cushion 7.8 mm long. The adaxial leaf cuticle is like the abaxial but has less regularly arranged stomata and epidermal cells of a more varied shape.

The margin of the free tip of the leaf consists of a sharp border of unicellular hairs, 90–100 μm long, 20 μm wide. These hairs are fused laterally for about three-quarters of their length, leaving only their rounded tips free, (Pl. 40, figs. 4, 7).

Genus CLASSOSTROBUS. Alvin, Spicer and Watson 1978

Classostrobus sp.A

Plate 41, figs. 1, 2, and 4

Description. Three compressed male cones were found amongst the foliage at God Nore. They are oval and 7.5–12 mm long and 6–6.5 mm broad. The microsporophyll heads are rhomboidal, up to 1.5 mm wide and 2.0 mm long, and appear to be spirally arranged. They are poorly preserved and neither microsporophyll stalks or pollen sacs were seen. (Pl. 41, fig. 4). Fragments of microsporophyll cuticle (Pl. 41, fig. 2) resembles *C. valdensis* leaf cuticle, but the stomata are less regularly arranged in files and fewer in number, e.g. 4 per mm. As on the leaves each stoma is surrounded by 5 subsidiary cells surrounding a stellate pit which is filled with 5 broad round papillae. The epidermal cells between adjacent stomata are isodiametric, with a mean width of 47 μm . However, the cells are somewhat elongate in 2–3 longitudinal rows between rows of stomata. Anticlinal walls are about 9 μm thick. Small blunt papillae are irregularly scattered across cuticle surface.

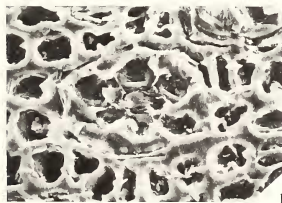
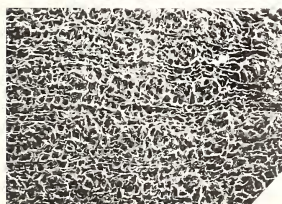
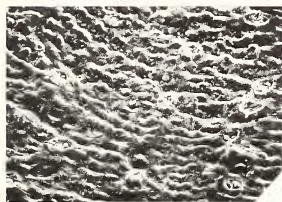
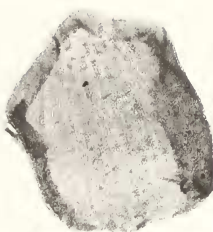
EXPLANATION OF PLATE 40

Cupressinocladus valdensis (Seward) Seward

Fig. 1. Shoot from the middle Purbeck Beds, Durlston Bay. PB:conf. 3. $\times 3$.

Figs. 2–10, 12, 13. Cuticle from the Great Dirt Bed, Holworth House, Dorset. 2, single leaf. $\times 10$. 3, triangular leaf tip with stomata in lower part only. SEM $\times 50$. 4, 7, marginal hairs of the leaf sheath. 4, SEM $\times 100$. 7, light microscope $\times 100$. 5, single stoma with strongly papillate subsidiary cells. light microscope $\times 400$. 6, outer surface of abaxial cuticle showing stomatal arrangement and slightly papillate surface. SEM $\times 50$. 8, 12, stomata from the same cuticle showing both level and rimmed apertures. SEM 8, $\times 300$, 12, $\times 250$. 9, inner surface of cuticle. SEM $\times 50$. 10, single stoma from fig. 9. SEM $\times 250$. 13, vertical section of stoma showing papillae inside stomatal pit. SEM $\times 280$.

Fig. 11. Shoot showing alternate branching, PB:conf. 1., basal Purbeck Beds, Portland. $\times 0.4$.



Although the pollen sacs are missing, isolated pollen grains were found adhering to the cone cuticle (Pl. 41, fig. 7). The pollen grains are spheroidal and slightly flattened at the poles, an equatorial diameter of 25–30 μm being reduced to 20–22 μm in this polar direction. A thickened belt, 6–8 μm wide and about 2 μm thick, encircles the equatorial region of the grain and bears 8–12 striations. Elsewhere the external surface is covered with small irregular granules. The internal structure is vermiculate. A small groove (the rimula) encircles the grain adjacent to the equatorial band on the distal side.

A pore marks the distal pole and is opposed by a triangular or trilete mark at the proximal pole.

Discussion

Wood. The type of wood described above which is the most common in the basal Purbeck Beds is assigned to the form-genus *Protocupressinoxylon* Eckhold on the basis of its mixed arrangement of tracheid pits, uniseriate rays, absence of resin canals but most importantly cross-field pits of cupressoid type.

Tracheid pitting intermediate in character between Araucaroid and Pinoid is common to many form-genera of Mesozoic wood constituting the Protopinaceae (Krausel 1949). In particular *Protocupressinoxylon* Eckhold is very similar to *Protopodocarpoxylon* Eckhold, species of which have recently been described by Lauerjat and Pons (1978) (*P. aveiroense*) from the Lower Cretaceous of Portugal, and wood of this type from the Wealden of the Isle of Wight by Alvin *et al.* (1981). Although in many respects these woods are very similar to that from the Purbeck they are distinguished by the cross-field pitting. In species of *Protopodocarpoxylon* Eckhold the cross-field pits are podocarpoid in the strict sense, with more vertically orientated apertures and are more numerous (up to 13 in *P. aveiroense* Lauerjat and Pons, up to 17 in the Wealden wood of Alvin *et al.* (1981)). In the Purbeck wood the cross-field pits are typically cupressoid (Pl. 39, fig. 6) with fewer, more regularly arranged pits with more horizontal apertures. They are characteristic of the form-genus *Protocupressinoxylon* Eckhold.

Previously described species of *Protocupressinoxylon* Eckhold have been listed by Attims and Crémier (1969). Although several species have similar tracheid pitting and abundance of resin and resemble the Purbeck wood, especially *P. lucombense* (Stopes) Eckhold and *P. vectense* (Barber) Eckhold (both from the Lower Greensand of the Isle of Wight) they possess vertical parenchyma, absent in the Purbeck wood. Species without vertical parenchyma include *P. dockumense* (Torrey) Krausel, *P. koeltitz* (Seward) Eckhold, and *P. malayense* Roggeveen, but are distinguished from the Purbeck wood by dissimilar medullary rays and cross-field pits. *P. chouberti* Attims and *P. aff. chouberti* Attims and Crémier are most similar to the Purbeck wood: vertical parenchyma is absent, growth rings are present, the tracheid pitting is a mixed arrangement of contiguous and separate pits and the cross-field pits are similar. However in *P. chouberti* Attims tangential pitting is present but notably absent in the Purbeck wood and in both these species the rays cells are twice as deep as those in the Purbeck wood. The abundance of resin found in the Purbeck wood was not noted in *P. chouberti* Attims.

The Purbeck wood is thus assigned to the new species, *P. purbeckensis* since in detail its features do not correspond with any previously described species. It is here considered to represent the wood of the Purbeck conifer which bears the *Cupressinocladus* (Seward) Seward foliage.

EXPLANATION OF PLATE 41

Fig. 1. Single shoots of *Cupressinododus valdensis* with male cone. Great Dirt Bed, God Nore Portland. $\times 1.4$.

Fig. 2. Cuticle from cone shown in fig. 4. Outer cuticles of several microsporophylls. Light microscope $\times 30$.

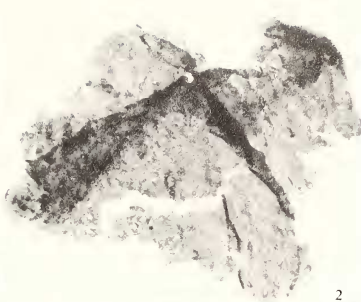
Figs. 3, 5, 7. *Classopollis* pollen associated with the male cone. 3, Grains clearly showing circumequatorial furrow. SEM $\times 1200$. 5, tetrad. Light microscope $\times 700$. 7, single grain showing equatorial striations. Light microscope $\times 1200$.

Fig. 4. Male cone *Classostrobus* sp. indet. PB:cone 1, Great Dirt Bed, God Nore, Portland. $\times 4$.

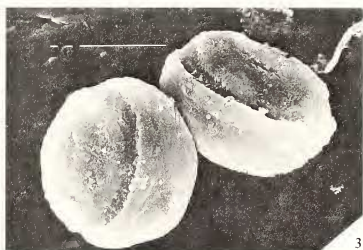
Fig. 6. Fine rootlets in the Lower Dirt Bed, Sheat Quarry, Portland. $\times 1.7$.



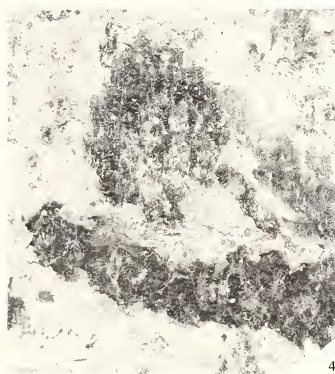
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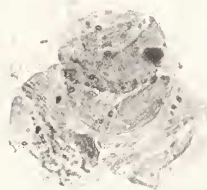
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Fossil wood of two other genera occur occasionally in the dirt beds. A few samples of fossil wood have unmistakable araucarian-type pitting (PB.8 from Blacknor, Portland and FF/2 from the Great Dirt Bed at the Fossil Forest at Lulworth). This wood has biseriate, even triseriate rows of hexagonal, alternately arranged bordered pits on the tracheid walls and is thus assignable to the genus *Araucarioxylon* Krausel.

One silicified trunk, PB.1 from the cliffs west of Anvil Point (text-fig. 2) and probably from the Lower Dirt Bed, has circular, separate bordered pits in uniseriate rows on the radial walls of the tracheids, small pits on the tangential walls and one or two large, simple pits per crossfield on the ray cell radial walls. Bars of Sanio are also clearly visible. This specimen is assigned to the genus *Circoporoxylon* Krausel.

Foliage. All the intact shoots from the Purbeck limestones mentioned above and the dispersed cuticle from the Great Dirt Bed have identical leaf arrangement in decussate pairs and similar cuticle structure.

The arrangement of leaves in opposite-decussate pairs is a diagnostic feature of the form-genus *Cupressinocladus*, originally erected by Seward in 1919 for vegetative shoots resembling those of modern Cupressaceae, and later emended by Chaloner and Lorch (1960), and Harris (1969). More recently Barnard and Miller (1976) emended it so as to exclude frenalopsid foliage where there are typically no suture lines between adjacent leaf bases. Shoots belonging to this form-genus have been described from the Jurassic and Lower Cretaceous localities worldwide, but the Purbeck specimens appear identical to *C. valdensis* (Seward) Seward from the English Wealden. No single Purbeck shoot has both good cuticle and well-formed branching pattern but the complete description above incorporated details from all specimens, and this agrees with that of the holotype, redescribed by Watson (1977). The cuticles sometimes differ slightly from the holotype in the presence of papillae on the epidermal cells which are absent on the holotype but intermittently present on the Purbeck cuticle. The cuticle surface of the holotype is featureless, the stomatal pits lying level with the surface, but in the Purbeck material stomata with both level apertures and encircling rims occur together in the same specimen.

C. ramonensis Chaloner and Lorch (1960) from the Lower Jurassic of Israel is very similar in appearance to *C. valdensis* (Seward) Seward but was considered distinct by the authors in having thinner cuticle, papillate epidermal cells and an even surface (they found that the stomata had rims on their preparation of *C. valdensis* cuticle). The leaf shape also differs from those of the Purbeck shoots in having a longer and more conspicuous free tip.

Two Lower Cretaceous conifers from Malaya, *C. malaiana* (Kon'no) Barnard and Miller (1976) and *C. acuminifolia* Kon'no (1968) look very similar but since the cuticles are unknown there is no strong evidence for identifying them with *C. valdensis* (Seward) Seward.

Oldham (1976) found *Cupressus*-like foliage in the Wealden marls at Swanage. His specimen 33 CuprCuA, is attributed to *Cupressinocladus* but is most unlike other published species, including the Purbeck shoots for, although the leaves are arranged in pairs, they have shorter decurrent bases so there is no conspicuous suture. The free tips are also much larger and rounder than on other species.

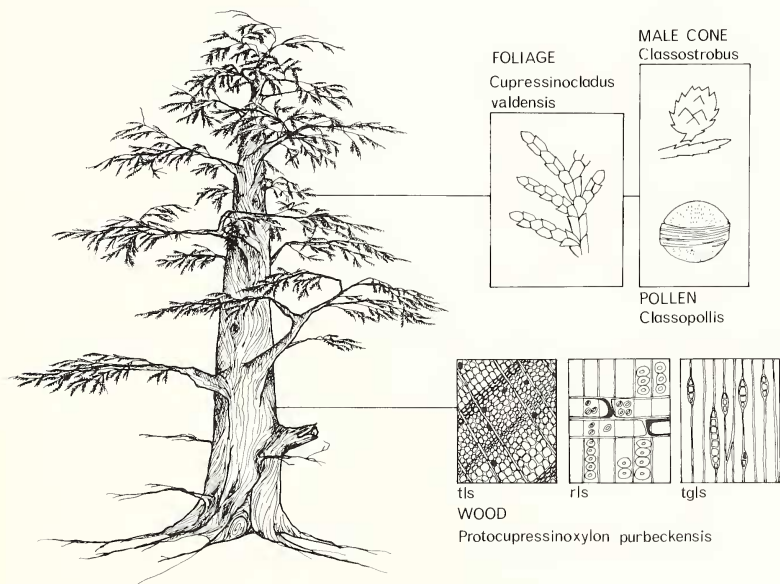
Male cones. The close association of male cones and *Cupressinocladus* foliage in the Great Dirt Bed at God Nore, supported by similarities in the cuticle of the microsporophyll and leaves, strongly suggests that they are part of the same plant. Several species of male cones associated with *Classopollis*-producing conifers have been described and Alvin *et al.* (1978) erected a new genus *Classostrobus* for male cones containing *Classopollis* pollen, and thus attributable to the Cheirolepidiaceae, but which were not specifically in organic contact with the shoots. Two male cones have been associated with *Cupressinocladus* foliage: *Classostrobus rishra* (Barnard) Alvin *et al.* with *Cupressinocladus pseudoexpansum* Barnard and Miller, and *Masculostrobus harrisianus* Lorch with *C. ramonensis* (Lorch 1968). The Great Dirt Bed cones are similar in shape and appearance to both of these cones, though slightly smaller in size, but lack of internal structure prevents further comparison.

Pollen. The pollen associated with male cones from the Great Dirt Bed is clearly *Classopollis*. In some cases the grains have not collapsed and exhibit remarkably distinct equatorial striations. Although detailed S.E.M. observations have not been made, it seems that the exine is very thin and the internal structure including the striations, is more prominent. Hence, of the many species described and illustrated by Reyre (1970) none is particularly comparable. Collapsed grains exhibit a surface structure of small granules, quite similar to that of *C. noeli* (Reyre) from the Upper Jurassic of Algeria, in the Sahara. Norris (1969) identified the *Classopollis* pollen from the Purbeck strata as belonging to 3 species, *C. torosus* (Reissinger) Balme, *C. echinatus* Burger and *C. hammenii* Burger; the pollen grains from the cone are most similar to *C. torosus*.

RECONSTRUCTION OF THE TYPICAL FOREST TREE

By virtue of the frequent occurrence of individual parts and their close association within the fossil soils, particularly the Great Dirt Bed, the wood, shoots, male cones, and pollen described here are considered to represent parts of one conifer which dominated the Lower Purbeck forests. This conclusion is strengthened by the apparent scarcity of other types of foliage and wood in these strata and agreement in cuticular structure between the male cones and leaves.

A few form-genera of fossil wood have now been attributed to the Cheirolepidiaceae on the basis of their association with cheirolepidiaceous foliage. In particular wood of *Protocupressinoxylon* type was considered by Harris (1979) to represent the wood of *Hirmeriella muensteri* (Schenk) Jung. Wood



TEXT-FIG. 3. Reconstruction of the dominant Purbeck conifer. The width of the base of the trunk represents a diameter of about 1 m.

of *Protopodocarpoxylo* type was associated with *Pseudofrenelopsis parceramosa* (Fontaine) Watson from the Wealden of the Isle of Wight by Alvin *et al.* (1981). Alvin *et al.* (1981) summarized the wood types attributed to the Cheirolepidiaceae. Their common features (contiguous and separate tracheid pitting, cupressoid cross-field pits and resinous tracheids and ray cells) are consistent with the characteristic features of the Purbeck wood.

As shown in text-fig. 3 the Purbeck conifer is considered to have wood of *Protocupressinoxylon purbeckensis* sp. nov., foliage belonging to the species *Cupressinocladus valdensis* (Seward) Seward and males cones (*Classostrobus* sp. A) yielding *Classopollis* Pflug pollen. Although the foliage has been classified as Cupressaceae in the past due to its similar appearance to modern species, *Cupressinocladus valdensis* (Seward) Seward was classified by Watson (1977) as Cheirolepidiaceae. Thus in summary, the affinity of the Purbeck trees to this family is supported by the cheirolepidiaceous-like wood and the *Classostrobus* cone, which on the basis of its *Classopollis* pollen is assignable to the Cheirolepidiaceae.

Additional information regarding the shape, size, and structure of these trees can be deduced from silicified tree stumps, branches, and trunks found in the dirt beds. Branches are seldom found attached to fallen trunks, even very long portions, presumably having broken off on impact with the ground or rotted away. However, at Chalbury Camp a small silicified branch, attached to the main tree stump, is preserved within the same mound of stromatolitic limestone as the rest of the tree (Pl. 38, fig. 1). Just over 1 m of the main upright trunk remains, rooted in the Lower Dirt Bed and attaining a diameter of 92 cm at the base of the trunk. The branch, 8 cm in diameter and 42 cm long, extends upward from the trunk at an angle of about 40°, at a height of only 44 cm from the top of the soil. On the main trunk of this tree, as on many trunk bases, the original positions of branches are indicated by the presence of numerous knots (buried branch bases) of both large and small diameters. Although not all may have penetrated through the sapwood, which has now vanished, some certainly did. The branches arose irregularly with no obvious whorled or spiral arrangement. Nevertheless the evidence suggests even in a full grown tree several branches arose from near the base of the tree, which probably had a more or less monopodial growth form. Radial sections cut across knots in silicified wood verify that the branches subtend an angle of about 40° with the main axis.

Many knots seen in thin section are encircled by cracks which contain soil particles and *Classopollis* pollen embedded in chalcedony. Other cracks with similar matter occur in the trunk wood. These cracks must have been open before silicification, either when the tree was alive or shortly afterwards.

The roots of these conifers are also preserved within the dirt beds. The bases of the erect tree stumps become thickened (but certainly not to the extent of being buttressed) and slightly twisted and then divide into roots spreading laterally through the soil in all directions. Silicified roots up to 10 cm in diameter extend from the base of the large tree into the Lower Dirt Bed at Chalbury Camp. The silicified parts are broken up into lengths of 10–15 cm but are still contained within a continuous lignitic sheath about 3 cm wide. Where the roots taper to less than 3 or 4 cm in width, the siliceous core is lost so the fine rootlets are preserved as lignite only. The root system here can be detected extending radially from the trunk for about 1 metre, though certainly the finer roots have been lost.

It was noticed long ago (Fitton 1836) that the tree roots could not penetrate the underlying hard limestone but were diverted laterally through the soil. The fossil roots appear to have grown down vertically as far as they could go but on meeting the limestone doubled back on themselves before finally extending horizontally through the base of the soil. Compressions of rootlets are present on the surfaces of pale, marly laminae within the Lower Dirt Bed in Sheat Quarry, Portland (SY689698) (Pl. 41, fig. 6). The ultimate branches of these roots are not particularly fine (0.7 mm diameter) and often terminate in small nodule-like swellings (0.6 mm diameter). By comparison with roots of modern trees it seems probable that they were mycorrhizae.

Although only pieces of trunk are preserved, some idea of the height of the Purbeck conifers can be obtained from the dimensions of the remaining silicified parts. Many straight trunks of about 6 m in length, some over 13 m long, have been observed (e.g. Fitton 1836, Mantell 1854) lying on the dirt bed. Dimensions of a tree trunk recorded by Fitton show that it tapers by only 9.5 cm from a diameter of 47.8 cm at the base to a diameter of 38.3 cm at a height of 5.51 m. With monopodial axes of this

length trees of over 20 m can be envisaged. The widths of the trunks and tree stumps also suggest that they were large trees; the mean trunk diameter of the sections measured being about 55 cm and the maximum recorded 1.3 m. However, because of the nature of preservation these values represent only part of the heartwood as the outer layers of the tree are always lost. None the less the bases of the tree stumps are often over 1 m in diameter.

Twenty trees showed growth rings which were mostly about 1 mm wide. Using this value and assuming the growth phases were annual, many trees from the Purbeck forests may then have had lifespans of at least 200 years and the largest would have probably been over 700 years of age.

Text-fig. 3 presents a reconstruction of the most common Purbeck conifer, based on the evidence outlined above including data on trunk diameters, frequency of knots, branching angle, etc. Clearly such a diagram involves an imaginative interpretation of the data and where direct evidence is not available comparisons have been made with modern conifers from semi-arid regions, such as *Juniperus oxycedrus* Linnaeus and *Cupressus macrocarpa* Hartweg.

PALAEOECOLOGY OF THE PURBECK FORESTS

The cheirolepidiacean conifer dominating the Lower Purbeck forests was thus a monopodial tree with spreading roots and branches and scale-like foliage, surviving perhaps for hundreds of years in relatively harsh, semi-arid conditions.

The anomalous association between hypersaline sediments on one hand and freshwater faunas, deposits, and large trees on the other could be explained by a strongly seasonal climate. The formation of evaporites suggests that semi-arid conditions prevailed in which gypsum and halite formed from hypersaline brines (West 1975). Algal stromatolites also flourished since the high salinity deterred grazing molluscs which would have destroyed them. However, for part of each year there must have been either sufficient rainfall for freshwater insects, molluscs, ostracods, and trees to thrive or else some other source of freshwater. At a palaeolatitude of about 36° N. (Smith and Briden 1977) a Mediterranean-type of climate seems most likely, with wet winters supplying water for tree growth but with rather long, dry summers in which lake salinity increased sufficiently for the formation of evaporites. This would also account for the ambiguous palaeoenvironment suggested by the lateral equivalent to the Great Dirt Bed at Portesham, represented by a chert horizon in which evaporite pseudomorphs are found with freshwater molluscs, charophytes, land plants, and ostracods. This deposit was suggested by West (1975) to represent a brackish or freshwater lake which, during summer droughts, increased in salinity and allowed halite to precipitate. A recent model for such a situation can be seen in ephemeral continental lakes and coastal lagoons in South Australia (Burne *et al.* 1980). Influenced by the semi-arid Mediterranean-type climate, the lakes become fresh or brackish in winter allowing plants (particularly charophytes), ostracods, and molluscs to thrive. In the summer season the low rainfall and high evaporation rate allows the saline water to become concentrated until gypsum and halite are precipitated. The land surrounding these modern ephemeral lakes is also forested.

This seasonal nature of Purbeck tree growth is clearly reflected in their growth rings. These are narrow and extremely variable in size suggesting that the conditions for growth varied considerably from one year to another. Large uniform cells of the earlywood zone terminate abruptly with a narrow zone of small, thick-walled latewood cells. False rings are also frequent. The picture that emerges is of a strongly seasonal climate in which tree growth was very sensitive to variations in climatic conditions. In some years relatively rapid growth was possible, but in others very little growth was achieved, probably because of low rainfall. A contributing factor must have been the relatively shallow rooting depth of the trees which meant that in a period of no rainfall they would rather rapidly experience the effects of drought. A striking feature of the foliage is the thick cuticle (15–20 μm). This is also consistent with the evidence for a rather xerophytic tree.

The environment suggested for the Purbeck trees is consistent with Vachrameev's view (1970) that the Cheirolepidiaceae were drought-resistant trees or shrubs dominating Upper Jurassic vegetation. Of the many ideas of habitat and form of the trees reviewed by Vachrameev (1970) and Srivastava

(1976), that of a coastal habitat is considered by many palynologists to be most likely. However, a criticism of any interpretation based on miospores alone is that a high concentration of dispersed pollen does not necessarily reflect local macrovegetation. This may be due to sorting in the depositional environment, resistance of particular grains to decay, etc. (See Chaloner 1968, Chaloner and Muir 1968.)

A mangrove-like community on river margins was envisaged by Batten (1974) and Oldham (1976) for *Classopollis*-producing plants in the English Wealden. However, Alvin *et al.* (1981) consider that the Wealden *Pseudofrenelopsis* was a large forest tree which, although living in a climate which seems to have been predominantly warm and moist, was adapted to withstand periods of drought in which it ceased to grow, producing very variable growth-rings.

An environment similar to that suggested for the Lower Purbeck forests can be seen today on Rottneist Island, on the West Australian Coast (Playford and Leech 1977). Here the Rottneist Island Pine (*Callitris preissii*) grows in shallow soils on limestones adjacent to salt lakes which dry out in summer, precipitating halite. Algal stromatolites encrust dead branches and rocks along the lake shores on which gypsum crusts also form. The island lies within the semi-arid, Mediterranean-type climatic zone and has a rainfall of about 700 mm, falling mainly during the winter months. Evidence from the sediments suggest that the mean annual rainfall during the Lower Purbeck was slightly less than this, probably about 400 mm.

SUMMARY

The Lower Purbeck forests were thus dominated by one species of conifer with tall, monopodial trunks, shallow spreading roots, and scale-like foliage. These conifers formed a closed forest bordering an hypersaline gulf, with only a few other conifers of different species and with probably sparse undergrowth. Their variable growth rings reflect growth in response to a seasonal climate which was probably of semi-arid Mediterranean type. The trees and freshwater faunas thrived during periods when freshwater was in ample supply but alternating seasons of drought allowed evaporites to form in the saline lakes.

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